SPECIES-FORMATION, OR THE SEGREGATION OF THE CHAIN OF LIVING ORGANISMS INTO SPECIES.[1]

THE DARWINIAN THEORY of selection furnishes no explanation of the formation of species. It contents itself with the assumption that intermediate forms perish because the newly originated, more perfectly adapted forms displant the old and less perfectly adapted ones. The indisputable objections which have been raised against this explanation are well known. Where the transformation is very gradual, as it is in the great majority of cases, the elimination of the intermediate forms, particularly if the modification affects only single individuals, is, owing to sexual intermingling, quite impossible without accompanying separation in space. But, as I have shown in the case of butterflies (*e. g.*, *Papilio Telesilaus*), new species do originate in the very heart of the distributional area of ancestral forms, and new species have unquestionably arisen everywhere, if not among yet alongside one another, without separation in space.

Darwin's selection cannot explain the transmutation of forms,

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[1] Extracts from an address on *Orthogenesis* (i. e., definitely directed evolution) delivered at the Third International Congress of Zoölogists at Leyden, September, 19, 1895; translated from Professor Eimer's MS. by T. J. McCormack. Professor Weismann's address which was delivered at the same Congress three days earlier and on a similar subject, appeared in *The Monist* for January, 1896, under the title *Germinal Selection*. It has seemed expedient therefore that the views of Professor Eimer, which represent the antagonistic position, should also appear in our pages. We regret that it was impossible to submit the proofs to Professor Eimer. —*Ed.*

nor the origin of new characters in forms; and no more can it explain the origin of species, despite the title of his celebrated book.

The origin of species can be traced to three main causes: (1) genepistasis, (2) halmatogenesis, (3) kyesamechania, all of which will receive their explanation in the following.

(1) By *genepistasis*, or cessation of development, I understand the halting of single forms at definite stages in the path of development whilst others move onward. *Epistasis*, the persistence or standstill of evolution at definite stages, is the main determining cause of the formation of species. It is solely through the operation of this cause that species are everywhere enabled to originate without separation in space. For orthogenesis, i. e., definitely directed and law-conforming evolution, produces the simultaneous transmutation of *numerous* individuals of the same species. And when a large number of individuals thus push onward in their developmental path whilst others remain behind, unavoidably a new species must originate. The evolutionary advancement of a large number of individuals can, therefore, take place in the very heart of the distributional area of the species, provided the advancing individuals are more sensitive than their fellows to the outward influences that condition the transmutation. But the farther the influences under consideration, viz., climatic and nutritional conditions, are removed from the centre of the distributional area of a species, the more powerful is their transformative effect. And the facts of variation for any given species do really show more aberrations and varieties as we recede from the centre of its distributional area, while still farther away new species are observed.

But, conformably to the law of *heterepistasis*, or the cessation of development at *different stages*, single characters may in transforming suffer suspension at a lower stage of development whilst others continue to advance. Heterepistasis appears to me a means of high import for insuring the stability of perfected species and one which is more determinative the higher and more complex the organism is. The interaction and interconnexion of so many widely diverse characters in their capacity as a totality is bound to insure the permanence of the whole for the reason that the characters in

question must necessarily counterbalance each other, seeing that by the very reason of their union as a whole each could not well be transformed by itself, just as in the pendulum of a standard clock the bars of different materials compensate each other during expansion and contraction.

On the other hand, simple organisms, in which few tendencies of development are as yet active, will give rise to less pronounced species, since here the developmental tendencies may even become reversed (*Foraminifera*).

But epistasis, or persistency of evolution at definite stages, is of paramount importance for the origin of species and varieties in the further respect that any individual characters whatever may in the course of enormously long periods of time make their reappearance by way of "reversion" as specific characters. For example, in the plumage of birds there sometimes reappear as specific characters markings which were specific characters in far distant and not at all immediately related ancestors or which only occurred in the down of such ancestors. We are concerned here, accordingly, not with ordinary reversion, which is an occasional phenomenon only and has nothing to do with the characterisation of new species, but with permanent reversion, with permanent phyletic reversion.

At times such old characteristics reappear only in one sex, particularly in the male, when we have permanent male phyletic reversion. Occasionally they appear only in some one part of the covering, for instance, in the ornamental part, or during transformation in the transitional part, when we have metamorphic or transformative reversion.

Such permanent reversion is to be conceived as epistasis or persistence, because the character in question, being according to the biogenetic law subject to repetition during individual development as an inheritance from ancestors, but being only fugitively repeated in the immediate progenitors of the retrogressive species and never making its appearance at all in the adult individuals,—this character, we say, persists and makes its appearance as a distinctive mark of the perfected species.

The explanation of ordinary reversion or atavism, personal

or individual reversion, is implicitly involved in the foregoing. There is concerned here merely the persistence or permanence of single characters, which according to the biogenetic law were obliged to appear only evanescently during ontogenesis, thereafter making way for others.[1]

Atavism is thus naturally classified with the remaining laws of persistence enunciated by me and is explained by them and the biogenetic law jointly. It is simply heterepistatic, ontogenetic, personal cessation of development.

Likewise permanent phyletic reversion is heterepistatic cessation of development—not ontogenetic but phylogenetic. We may characterise the two species of reversion most simply as ontogenetic and as phylogenetic reversion, or as ontogenetic and phylogenetic epistasis or heterepistasis. Both differ from the species-originating process known as genepistasis by the fact that genepistasis signifies a cessation of all the characters embraced by a given definite direction of evolution, the arrestation lying entirely outside of ontogenesis. We enter here again the domain of orthogenesis to which both ontogenetic and phylogenetic reversion ultimately belong.

The biogenetic law,[2] also, is the expression of definite directions of evolution in so far as these have not been altered by the use or disuse of organs in ancestors. Naturally it holds good not only for ontogeny but also for metamorphosis or the period of development persisting after birth or after emergence from the egg. We see here, for example, in the markings of lizards, how one marking is replaced by another in the direction from behind forwards (postero-anterior development, law of undulation), and how the females usually preserve the youthful characters longest or for good, whilst the males first assume new characters (male preponderance). Male

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[1] Compare H. Kohlwey, *Das Gesetz der Vererbung*, *Blätter für Geflügelzucht*, 1886, where the same idea is uttered.

[2] Hyatt is of opinion that the biogenetic law was discovered not by Haeckel but by Agassiz. As a matter of fact, it had been previously clearly and definitely enunciated by Kielmeyer, Mechel, and other Germans. Compare also Schopenhauer, *Parerga*, II., p. 168.

preponderance is simply the advance of the male one evolutionary step further along the path of orthogenesis. In numerous animals investigated by me, the old original characters are found permanently at the front in a fully perfected state, whilst the new ones are found at the rear; as in the markings of lizards, of birds of prey, Papilionidæ, etc. In the sculpturing of ammonites and snail shells the old characters are found on the most primitive whorls, the new characters on the whorls that appear latest.

Perfectly analogous examples may be adduced for plants with respect to the succession of leaves.

A second important cause of the segregation of the natural chain of organisms into species is:

2. *Saltatory development* or *halmatogenesis*, which consists of the sudden, unsolicited appearance of new characters, or, where a large number of such new characters appear, of the sudden origin of new forms that deviate widely from the ancestral form. To what extent direct outward influences are operative here is demonstrated by many facts, such as the sudden, *kaleidoscopic* transmutations of the markings and colorings of butterflies through the agency of heat or cold during development (including horadimorphism or seasonal aberration), the sudden transmutations due to nutrition or general outward conditions of life, as those determinative of the origin of *Amblystoma*. So, too, the conversion of *Artemia salina* into *Branchipus* (Schmankewitsch) shows sudden, graded transmutations. Everywhere here correlation appears as one of the most effective causes of the transmutation of forms.[1]

That separation in space is an influential factor in the origin of species follows immediately from my doctrine of the genepistatic formation of species, and from the effect of outward influences upon transmutation.

Outward influences in their action on genepistatically segregating forms are enhanced as to species-creating power, or as to their power of promoting the creation of species, according as

[1] A distinction is to be made between the kaleidoscopic correlation which is here operative and the functional correlation of Cuvier which relates to the use of parts

separation in space keeps the originating species and the ancestral species absolutely apart, or absolutely prevents sexual intermingling. But no direct, independent significance can be accorded to separation in space as a factor in the formation of species.

As already said, the formation of species may take place in the very heart of the distributional area of the ancestral form, and so be conditioned solely by genepistasis.

Of the highest significance for the formation of species without separation in space, however, is the following factor:

3. *Kyesamechania*,[1] or hindrance to impregnation, the inability of a certain group of individuals to impregnate others than themselves, due to morphological or physiological changes in the seed or ovum or both, or to a change in the time of maturity of the seeds or ova. Changes of this kind occur mainly through correlation, through indirect influence on the sexual organs.

I referred to the phenomenon of prevention of impregnation as early as 1874.[2] Some time later (1886) George J. Romanes lighted upon the same idea and under the name of physiological selection contrasted prevention of impregnation as a factor in evolution with the origin of species by natural selection.[3]

The main factor, finally, that conditions and promotes the formation of species is the activity, the continued use of certain organs. The same result may be obtained by intercrossing, though ordi-

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[1] From κύησις, impregnation, and ἀμηχανία, incapacity.

[2] First in *Zoologische Studien auf Capri. II. Lacerta muralis coerulea*, Leipzig, Engelmann, 1874, p. 45. Then in *Zoolog. Unters. mit bes. Berücks. d. Biologie, I. üb. Bau u. Bewegung d. Samenfaden*, Würzb., Stahel, 1874, p. 42, and *Würzb. Verh.*, 1874. Also in *Variiern d. Mauereidechse*, 1881, p. 257, and in *Entstehung d. Arten*, I., p. 45. In prevention of impregnation there are concerned, according to my opinion, the two following factors: (1) mechanical causes, involving (not to mention such as are founded in the rough structure of the sexual organs) (a) the size of the spermatozoa or the breadth of the oviducts or the varying stoutness of the integuments of the ova, and (b) the varying power and form of movement of the spermatozoa which according to my observation is in vertebrates performed in screw-like motions mostly rotatory. The spermatozoa are, in fact, in closely allied species widely different as to shape and movement. (2) Physico-chemical differences in the composition of sperm and ovum.

[3] *Journal of the Linnean Society*. Zoölogy, London, 1886. *The Monist*, Vol. I., No. 1.

narily this has a levelling and hindering effect in the formation of species.

As for the rest, species are not originated by natural selection but already existing species are preserved by natural selection.

I accept in this unreservedly one part of Darwin's conceptions, as it is stated in the inscription of his book on the origin of species which reads: "The origin of species by means of natural selection, or, the *preservation of favored races in the struggle for life.*"

DEMONSTRATION.

I shall extract the proofs for the views which I have here enunciated, from the facts furnished in my *Formation of Species and the Relationship of Butterflies*, as found in the recently published second part of this work, containing "the forms allied to the Swallowtails."

I distinguish between three groups of Swallowtails: the *Turnus*, *Machaon*, and *Asterias* groups. These groups contain mostly American forms and preponderantly North American forms. *Alexanor* alone in the *Turnus* group occurs in Europe and Asia; the *Machaon* group is represented in Europe, North America, Asia, and Africa. Further, all three live in connected distributional areas and are also all three immediately connected in relationship. The North American *Papilio Eurymedon* belonging to the *Turnus* group, or some similar ancestral form of this same group, forms the starting-point of all the others and at the same time connects them with the *Segelfalter* (*Papilio podalirius*). The relationships involved are mainly inferred from the markings, but the other characters all follow these: venation does not appear to be entirely determinative of the markings. We can tell from the markings, coloration, and shape at once that relationship follows geographical distribution, the fact being that at every remove from the main seat of the phyletic types no matter how small, the forms represent more and more distantly related varieties or species. As we have already demonstrated in the case of the *Segelfalter*, so also in the case of the *Swallowtails*, as a glance at the Plates of the last-named work will show, variations of individuals pass in adjacent areas into aberrations, and in more remote areas into species. The same Plates

(*Swallowtails*) also show that everywhere definite directions of development are determinative of the transmutation. By them are produced, first individual modifications in single forms of a species (aberrations), then varieties, and finally again, species. Now all these directions of development which lead to the origin of aberrations, varieties, and species, have nothing to do with origin by natural selection, nor with sexual selection. The new forms arise without the least regard for utility; every new form of butterfly shows for itself the absolute impotence of natural selection. On the other hand, the facts of geographical distribution with respect to relationship show very distinctly that outward and especially climatic conditions must have been coincidently determinative in the formation of species. This is proved by the fact that *artificial temperatures produce exactly the same directions of development or modifications thereof as the same butterflies exhibit in their actual geographical distribution.* This has been recently shown with perfect clearness by the researches of Standfuss, who by causing heat to act on the pupæ of *Papilio Machaon* in Zürich, produced butterflies such as are found in August in Syria. And here not only changes of coloration and marking but also those of shape as produced by heat in the pupæ agree with the southern forms.

Additional proof of the correctness of my view is furnished by the facts of seasonal aberration, and first by the fact that the summer forms everywhere correspond to the forms artificially produced by heat, and secondly by the fact that the characters of the summer forms of species living farther towards the North are the same as, or closely similar to, the distinguishing characters of allied butterflies which live in the South.[1]

The experiments of Standfuss, Merrifield, and Fischer, as well as the facts which seasonal aberration furnish, show that the explanation which Weismann has advanced regarding the origin of *Vanessa Levana* being a reversion cannot hold water, that this is also true of his explanation of the origin of the dark form of

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[1] Compare especially the first part of my *Schmetterlinge*, Sec. "Die Segelfalterähnlichen."

Polyommatus Phlæas, and finally that in all the consequences of the action of heat and light on butterflies we are concerned simply with the *inheritance of acquired characters*, which it was his special object to overthrow.

"On the plates of my butterflies the formation of species and the laws of evolution can be read directly from the wings. The markings and colorings of the same are so many letters speaking a clear and forcible language that no one who wants to know the truth can misunderstand. Like the leaves of an open book the written characters on the wings of our butterflies show their past and present history."

"Here on the tablets of the laws which living nature has placed in our hands, the truth of evolution lies written, and not in the writings of the naturalist philosophers who dream their evolutionary fancies with an utter disregard of the facts, and who scatter them among their credulous followers in unremitting profusion. Mind-made hypotheses are not investigations of nature. No hypothesis is justified in natural inquiry unless it rests upon facts. The man who scorns facts is no natural inquirer." Such were my words in the Preface to my *Swallowtails*.

This handwriting tells us in the most convincing and palpable manner, how one species passes into another, and how the species are segregated. Nowhere has the actual origin of species and the connexion of a concatenated series of species been hitherto so forcibly exhibited and demonstrated as here.

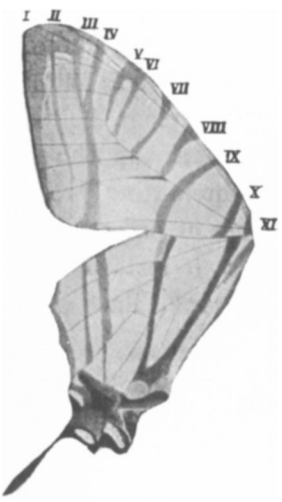
Let us look at the facts more closely.

In the first part of my *Artbildung und Verwandtschaft bei den Schmetterlingen*, in the Section on *Die segelfalterähnlichen Papilioniden*, I have derived the last-named butterflies from forms which had eleven longitudinal stripes on their wings, such as are still shown to-day by certain species like *P. Alebion*, *Paphus*, *Glycerion*. Now these longitudinally striped[1] butterflies give, as I am becom-

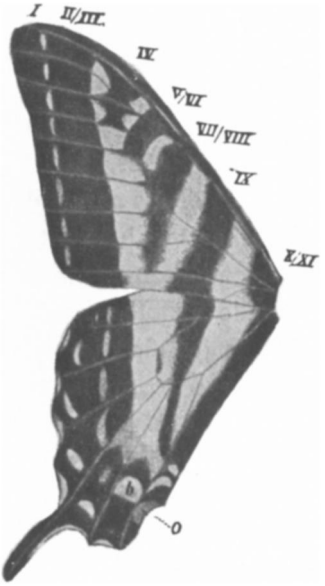
[1] The objection has been raised on many sides that what I call longitudinal striping in butterflies is really a transversal striping of the wings. And this is quite correct if we speak of the marking of only a single wing. But I speak of the marking of the entire butterfly, of its body, and its two wings, of the front and the hind

ing more and more convinced, the fundamental form of marking of all diurnal butterflies. Partial or total disappearance, broadening and fusion of the fundamental bands condition the formation of the characteristic marks of aberrations, varieties, species, and families. From the transformations of the fundamental bands and the intervening spaces, the ocellated spots also are produced.

In the majority of *Segelfalter* some of the eleven bands have already disappeared or have been shortened from behind forwards.



Cut 1. *Papilio Alebion* GRAY.



Cut 2. *P. Eurymedon* BOISD.

The case is similar with those Swallowtails which are their nearest relatives.

I reproduce here a representation of *Alebion* from above[1] with

wings as integral parts of a whole. That the wings are a whole with respect to marking is proved by the connexion of the marking in front and behind, in the position which the wings assume when spread out and where the marking and the coloration, owing to the hind wings being covered by the fore wings, are partly wanting. The connexion in question is likewise proved by the mode of transformation or disappearance of the markings from behind forwards, from the hind wings to the fore wings; in other words, by the existence of general laws of marking in such transformation. For details see my *Artbildung*, II., 48, 49.

[1] In the following cuts the left wings always give the upper sides, the right wings the under sides.

its eleven fundamental bands marked by capital Roman numerals, designations which I have everywhere employed in my *Artbildung und Verwandtschaft bei den Schmetterlingen*, and which I shall also lay at the basis of the description to follow. For all the markings of the diurnal butterflies can be traced back to these bands and to the black coloration of the veins.

Also the following cuts of the Swallowtails have been taken from my *Artbildung*. In the footnotes added to the descriptions will be found numbers and plates referring to the corresponding colored cuts of the last-mentioned work.

The form of living Swallowtails which in most likelihood is nearest allied to the initial form of the group, and which is most nearly connected with the *Segelfalter*, namely *Papilio Eurymedon* (Cut 2), has as yet only seven longitudinal stripes; the remaining ones have partly disappeared and have partly been fused at the sides. As in the *Segelfalter*, they disappear in the succeeding species, by orthogenesis, from behind forwards, conformably to the law of postero-anterior development, *Papilio Turnus*, *P. Alexanor*, *P. Machaon*.

In *P. Alexanor* there are, as Cut 3 on p. 108 shows, still seven stripes present either in part or in whole, I, II, III, V/VI, VII/VIII, IX, XI. V/VI is, here as always, situated on the fore wings at the outer border of the middle cell. IX forms with XI an angle, and is on the under side frequently colored black, white, and red, or black, white, and yellow ("ornamental band"). *C* on the outer border of the middle cell of the hind wings like V/VI is here as in other families, *e. g.*, in the Pierids, an extremely important marking, in its origin probably a component part of VII/VIII, which in some *Segelfalter* reappears rudimentarily but in the Swallowtails is a pronounced "*C*-marking."

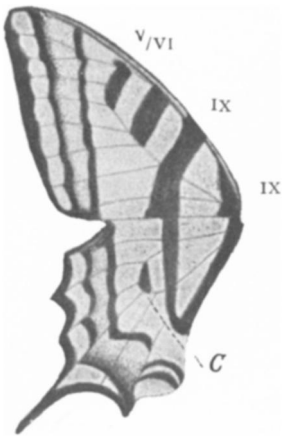
The remaining transformations of the bands of Swallowtails are the consistent expression of the general law of markings, first in that they exhibit spots which are due to abridgement and lateral fusion as in *P. Machaon* in Europe and North America,[1] and further

[1] Plate VI. Fig. 8.

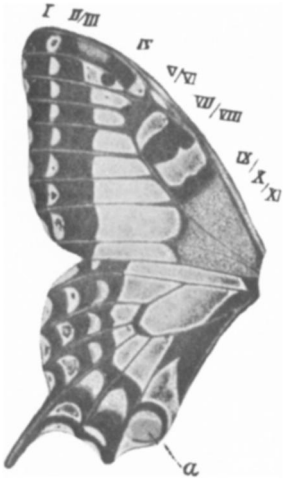
in that they show rudiments of transversal stripings induced by the blackening of the cross veins (noticeable in other specimens of *Machaon*). These rudimentary transversal stripings are by other agencies subsequently perfected, as in the case of *P. Xuthus* and *Xuthulus*.[1] Here, on both sides of the wings, and that, too, in the forward middle cell, a transversal striping makes its appearance (*a*, Cut 5).

In *P. Hospiton* (Cut 7) there is a rudiment of this new marking present.

Finally unicoloration arises, as follows. The dark coloring



Cut 3. *Papilio Alexanor* Esp. ♀.



Cut 4. *Papilio Machaon bimaculatus* m.

which has made its incipient appearance at the inner wing-angle of *Machaon* extends systematically outwards over the wings and ultimately covers their entire surface, excepting a few spots at the border (*Asterias* group, Cut 6).[2]

We have accordingly a simplification of marking and coloring in the higher forms and not a perfection, as Nägeli's theory and as sexual selection would require. The same holds true of the tails of the hind wings which in the higher forms are not lengthened but shortened. And both facts hold true of the *Segelfalter*.

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[1] Plate VI. Figs. 9 and 10.

[2] Plates VII. and VIII.

The directions of development of these markings show accordingly in their systematic conformity to law the same detailed tendencies as are determinative in animals quite unallied to the butterflies, as in mammals, birds, lizards, mollusks, etc.

The gradual transformation of the markings takes place therefore, as the cuts and particularly the plates of my book show, for the most part through the disappearance, shortening, and lateral fusion of the bands, in which process the upper side as a rule is considerably in advance of the under side which largely retains

Cut 5. *Papilio Nuthus* L. (Under surface.)

Cut 6. *Papilio Asterias* Cram. ♀.

the earlier and more primitive condition,—a result the very reverse of that demanded by the theory of adaptation for diurnal butterflies.

In addition, new bright colors and color-markings and embellishments make their appearance, at first mostly as before on the upper surface, as the bright blue inner marginal band which conformably to postero-anterior development first appears at the back and developing itself on the hind wings afterwards advances forwards (*P. Turnus*, Plate V, *Machaon*,[1] *Asterias*-group[2]). And if

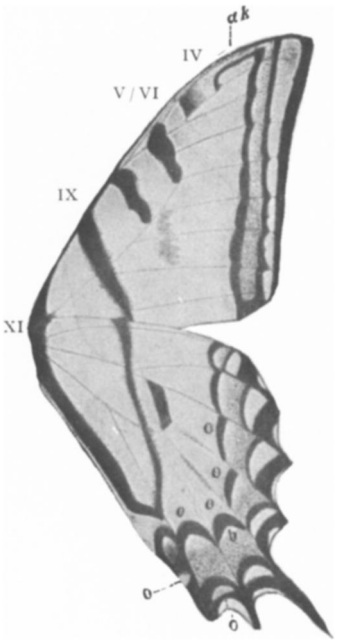
[1] Plate VI. [2] Plate VII.

this band is more pronounced and more beautiful on the under side than on the upper, on the other hand it did not make its appearance there until subsequently when it was either on the verge of disappearing above or had already disappeared (*P. Troilus*,[1] *Palamedes*[2]).

At the inner angle of the hind wings, the ornamental hinder eye, as in the *Segelfalter*, is developed from portions of the mar-

Cut 7. *Papilio Hospiton* Géné.
Under surface.

The three *o*'s on the hind wing indicate the points where orange-red (reddish-yellow) spots lie.



Cut 8. *Papilio Daunus* Boisd ♂.
Under surface.

The four *o*'s on the interior of the hind wings show the places where orange-red spots are situated.

ginal bands, as comparison with the more primitive under side frequently shows, e. g., *Papilio Hospiton* (compare Cut 7 at the point *o* outside the Cut).[3]

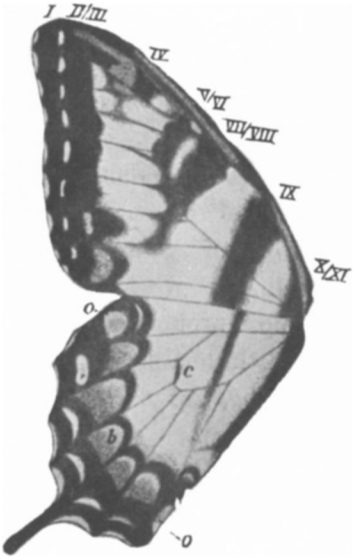
Quite remarkable is the slow, systematic production from a fragmentary black band, of a black nucleus in the orange-red hinder eye, particularly in *Machaon* and *Asterias*. Whilst the upper side

[1] Plate VIII. Fig. 2, [2] *Idem*, Figs. 3 and 4, etc. [3] Plate VI. Fig. 6.

is usually in advance of the under side in development, the reverse also takes place, as, for example, in the production of orange-red spots, which again originate first on the posterior part of the hind wings within the innermost black marginal band in the cells of the wing on the under side,[1] as in *P. Machaon* and in *P. Hospiton* (*o*, Cut 7),[2] and further in *P. Turnus*, *Daunus* (the four inner *o's* on the hind wings of Cut 8[3]), and which gradually increase in intensity of color and in magnitude, to spread finally over the wing cells of the

Cut 9. *Papilio Asterias* var. *Calverleyi* GROTE.

The *o*'s indicate two series of reddish-yellow spots. The *a* shows the nucleus of the hinder eye-spot.



Cut 10. *Papilio Turnus* L. ♀.

fore wings (*P. Brevicauda*, *P. americus*, *P. Hellanichus*[4]). In the last-named butterfly they are also present on the upper side, as they are in *Calverleyi* (*o* on the hind wing, and corresponding neighboring spots, Cut 9).[5]

It is noteworthy of *P. Turnus* that these spots appear first more prominently in the female.[6] In *P. Bairdii* the reverse is the case.[7]

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[1] Plate V., VI. [2] Plate VI. [3] Plate V. [4] Plate VII.
[5] Plate VIII. [6] Plate V. Fig. 2. [7] Plate VII.

Similarly in the sulphur-yellow spots of the outer marginal band orange-red dots make their first appearance underneath (*Turnus*). In the higher forms these spots are found only in the cells of the fore wings and have disappeared (Cut 9) in the two hind wings (*P. Asterioides* and *Asterias*).[1] The foremost of these spots is in *Turnus* carried over to the upper surface (compare Cut 10, the *o* to the front), as also in *Troilus*;[2] and in the same place, as also rudimentarily in the remaining cells of the hind wings as well as in the hindmost cell of the fore wings, a like coloring appears also in *P. Machaon asiatica*,[3] and it is this coloring that everywhere produces the orange-red of the hind eye-spot in the innermost cell of the hind wings (e. g., *o* in *Turnus Glaucus* ♀, Cut 19, *a* in *Papilio Bairdii* ♂, Cut 15).

An extremely remarkable direction of development in the transformation of the markings is manifested in the fact that on the under surface of *Machaon* rudiments of that streaking of the middle cell of the fore wings first appear which in *Xuthus* and *Xuthulus* become more pronounced in development, are present on both sides, and constitute a prominent characteristic of this species (compare *P. Hospiton*, Cut 7, *P. Xuthus*, Cut 5, and *Hippocrates*,[4] also *P. Machaon æstivus*).

Numerous other systematic and law-conforming transformations of marking and coloring might readily be cited.

Instead of doing so, however, we shall proceed to examine a few *newly appearing* characters in our Swallowtails.

The new characters in question make, as I have already shown for the *Segelfalter*, their first appearance in a very inconspicuous and scarcely perceptible manner. Like all other modifications they are first produced in single butterflies of a species only as aberrations, then they appear as characteristics of varieties, and finally as marks of species.

In this manner certain tiny black dots make their appearance in the cells of the fore wings of Swallowtails, at first partly as marks

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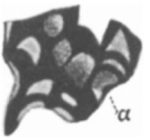
[1] Plate VII. [2] Plate VIII. Fig. 2. [3] Plate VI. Fig. 7. [4] Plate VI.

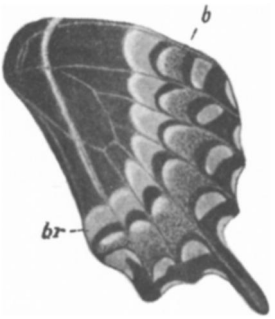
distinguishing aberrations and partly even as such distinguishing species.

For example, in the forked cell of *Machaon* there is found, usually at both sides, but always on the upper surface, a black point or spot, which is also present and has become a mark distinguishing the species in *Xuthus* and *Xuthulus* and in several members of the *Asterias* group (compare *P. Hospiton*, Cut 7, at *G*; *P. Machaon bimaculatus*, Cut 4; *P. Xuthus*, Cut 11; *P. Bairdii* ♂, Cut 15). In *P. Turnus* ♀ and in *P. Alexanor*, etc., there is found in place of

Cut 11. *Papilio Nuthus* L. (Upper surface.)



Cut 12. *Papilio Machaon asiatica* Mén.



Cut 13. *Papilio Palamedes* Drv. ♂.

Hind wing, under surface. *br*. brownish-red. *b*, blue (blue marginal band).

this an outwardly protruding fragment of band IV.,[1] from which it has doubtless originated. In many *Machaon* (e. g., *Hospiton*) the black spot acquires as a new character a bright space in its centre (compare the cut).

So also in the bright interior of the first lateral margin-cell which lies just behind the forked cell, is sometimes found a very

[1] In the address as printed in the *Compte-Rendu*, page 163, band IV. reads erroneously band V/VI.

small but very distinct dot in some of our native *P. Machaon* (compare *P. M. bimaculatus*, Cut 4). It is likewise found in a butterfly of Allahabad.[1] In *P. Xuthus* (compare Cut 11) it is always present on the upper surface and only seldom as a small transversal streak; it is usually found as a large oviform spot, and from the marking which appeared in *Machaon* as an aberrational phenomenon it has in this last stage been converted into a conspicuous and distinguishing mark of the species.

A new phenomenon is the appearance of a dark outward border on the middle cell of the hind wings, which on the under surface of *Turnus* occupies the entire outer margin, but on the upper surface makes its appearance only as a black line of varying shortness —the *C*-marking as I have termed it and which is very conspicuous for example in *P. Turnus* ♂ (Cut 10 *C*), *Daunus* (Cut 8), *Pilumnus*, but particularly in *Alexanor* (Cut 3 *C*). In *Daunus* ♀ it is present only on the under surface; in the majority of *P. Machaon* the entire border of the middle cell is black also on the upper surface, as it is also in the majority of *Asterias*.[2]

Another new character is the black nucleus in the hinder eye-spot which is already pronounced in appearance in many members of the *Machaon* group, e. g., *P. Zolicaon* and *P. Machaon var. oregonia*, and then in *Asterias*, and whose origin from a fragment of marginal band has already been mentioned. We recognise the first stage of its production in Cut 19 representing *P. Turnus Glaucus* ♀, just above the letter *g*; in *P. Machaon asiatica* (Cut 12) at the letter *a*, and in *P. Palamedes* ♂ (Cut 13 representing the under surface). A more advanced stage is seen in *P. Bairdii* ♂ (Cut 15), to the right above *a*. The nucleus of the hinder eye-spot is completed, that is, perfectly marked off, in *P. Bairdii* ♀ (Cut 18), *T. asterioides* ♂ (Cut 16, both times at *a*), *P. Xuthus* (Cut 11), etc.

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[1] Compare for the case of *Machaon* Cut A at page 26 of my *Swallowtails*.

[2] Colored and even red borders of the outward angle of the middle cell of the hind wings were observed even among the *Segelfalter* in the case of *P. Protesilaus* (*Segelfalter*, Plate I. Fig. 5), but without assuming any further import. As for the rest it was pointed out that the *C*-marking was probably a reappearance (reversion) of a fragment of band VIII.

A new and very marked character, distinguishing the majority of Swallowtails in the broadest sense, finally, is the blue marginal band, the blue spots of which are marked *b* in a number of the following cuts (*P. Bairdii*, *Turnus Glaucus*, ♀ *Palamedes*, *Daunus*, *Asterias*).

Part of these new characters, which in the end appear as fresh marks distinguishing the species, is accordingly to be regarded as a transformation of old characters, whilst another part is entirely new.

Now these new characters, viz., the tiny dots and lines here making their first appearance, can be observed in their first, primitive origin, and can be followed in their development from almost imperceptible markings as they appear here and there in individuals of a species, until they have become fixed as permanent marks of a different species. The ids and determinants of Weismann cannot be seen. But one can palpably and irrefutably see in the faint dots here considered that the transmutation and origin of a species has taken place in diametrical opposition to the theory of determinants. The same is proved by all transformations of existing characters into new distinguishing marks of species. The origin and perfection of new characters, the transmutation and origin of species, take place conformably to law in a few, quite definite directions without any "oscillation"[1] whatever, without any reference to utility; they demonstrate, in fact, the absolute impotency of natural selection in this domain.

One can read from my plates how all the characters of the different varieties and species of swallowtailed butterflies have arisen one from another by orthogenesis. Every variety or species is distinguished by a definite total of characters which have originated orthogenetically from the most inconspicuous beginnings, which through heterepistasis on the one hand, homöogenesis on the other, and finally through halmatogenesis, have been developed and compounded now in this manner, now in that; whilst the upshot of the whole shows that the origin of species essentially re-

[1] See *Germinal Selection*, p. 20, where Weismann contends that the variations presented to selection "oscillate" about a given zero-point.—*Trans.*

poses on genepistasis or cessation of development at different single stages of the evolutionary advance, the process being that one species thus always presents a higher stage of development in its characters than another.

That utility plays no part whatever in the process follows from the nature of the determinative characters themselves, but is particularly demonstrated by the following considerations: (1) In different species of the same phylogenetic line, the various stages of these characters never occur in the same perfection or arrangement; (2) they are equally determinative in different parallel chains of species; (3) they also occur side by side in different sexes in different development; (4) they occur in the same development in different species of one phylogenetic line—apart from the fact that (5) they everywhere make their appearance in the most inconspicuous beginnings, are preserved in faint forms of perfection as distinctive marks of species and may disappear again, and that (6) the complete reversion of all characters so originating, or their concealment through being colored black, that is perfect simplification, may arise.

The significance of heterepistasis for the origin of species is everywhere forced on our notice by my cuts, and I shall draw attention here only to a few special conspicuous features.

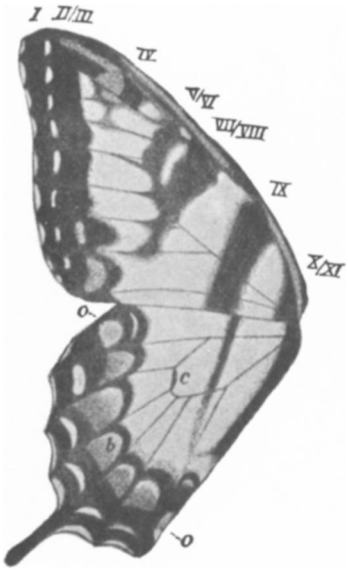
In *Machaon* the uniform black coloration of the upper surface of the roots of the forewings has become characteristic of the group. In *Xuthus* and *Xuthulus* this character has not reached its full perfection, although the reverse is the case with the striping of the middle cell of the fore wings, which is rudimentarily indicated only in a few *Machaon,* not having attained there further development. *Hellanichus* receives a very special character from the running over of the orange red color-spot on the under surface of the wings to the upper surface. The *Turnus* have lost much of their original marking, in that the original longitudinal stripes have been not only shortened from behind forwards, but also diminished in width. Particularly the male of this butterfly,[1] which has advanced quite

[1] *Artbildung*, Plate V. Fig. 6.

far in transformation, has been made very bright in this manner. Also in *Machaon* the longitudinal stripes have disappeared from the back to the front, but in this instance the black coloring of the transverse veins has set in.

The widening of the residual stripes of the fore wings and the black coloration on the upper surface of the roots of the same by the fusion of the longitudinal stripes points to a direction of development which is the opposite to that in *Turnus*.

This last direction of development, the appearance of a uni-



Cut 14. *Papilio Turnus* L. ♀.

Cut 15. *Papilio Bairdii* Edw. ♂.

form black coloration on the roots of the fore wings, which even in *Machaon* had begun to extend to the hind wings, continues to spread in *Asterias* to both wings, and in the *Asterias* group makes for unicoloration or perfect black coloration. This progressive blackening offers, coincidently with two instances of saltatory development (halmatogenesis), conspicuous examples of independent similarity of development, homöogenesis, and of female preponderance, whereas otherwise male preponderance is usually determinative. The same phenomena suddenly assumes in *Bairdii* ♀ and in *Turnus var. Glaucus* ♀ so advanced a stage as to ex-

tend over the entire wings with the exception of a few spots, whereas the average female of *Turnus* is sulphur-yellow in its ground color like the male, and whereas in the males of *Bairdii* the black coloring is only somewhat more extended than in *Machaon*. In other words, the phenomenon which in *Bairdii*♀ and *Turnus Glaucus* spasmodically and suddenly developed, and only in the female, was, beginning with *Machaon*, gradually perfected in the *Asterias* group in both sexes. The black coloring kept extending here from species to species, beginning at the roots of the wings and spreading over their entire surface, at last leaving be-

Cut 16. *Papilio asterioides* Reak. ♀.

b and the three spots situated in the wing cells just above are blue (blue marginal bands).

Cut 17. *Papilio Asterias* Uram. ♀.

hind it only bands of spots of the ground color,—the same as were left in *Bairdii*♀, whilst in *Turnus Glaucus* even these were lost.

The butterflies represented in Cuts 14 to 19 show accordingly a series of different stages of law-conforming transmutation of species, which exhibit not an advance towards beauty and variety, but an advance towards simplicity, towards dark and sombre colorings, such as I have described among the *Segelfalter*, and such as appear widely distributed as we shall see later on among other groups of butterflies. Sexual selection, as being on the face of it absolutely excluded so far as the markings and coloration of butterflies are concerned, is nowise involved here, nor is there any

ground for believing that selection or adaptation is in any way concerned.

The species *P. americus*, *Nitra*, *Indra*, *brevicauda*, *asterioides*, and *Asterias* figured on Plate VII. of my *Schwalbenschwanzähnliche Schmetterlinge*,[1] show a complete serial line of transformations within the *Asterias* group, and are at the same time conspicuous examples of genepistasis. The highest degree of transformation in this series has been reached by *Asterias*, a species which is almost as far advanced as *Bairdii*♀. *P. Troilus*[2] is almost as far ad-

Cut 18. *Papilio Bairdii* Edw. ♀.

Cut 19. *Papilio Turnus Glaucus* L. ♀.

vanced on the other side and represents an instance of heterepistasis as does also *Palamedes*.

We have figured still another butterfly which is most likely a conspicuous instance of halmatogenesis: *Papilio Asterias var. Calverleyi*, Cut 9,[3] which according to Edwards is probably a cold form of *Asterias*. It has been transformed towards the *Machaon* type in

[1] The cuts given in the present article are in fact a makeshift only, for the purpose of explaining the description. I must refer to the plates of my *Artbildung*, etc., for a full understanding of the facts.

[2] Plate VIII. Fig. 2. [3] Plate VIII. Figs. 5 and 6.

such wise that the black occupies only the inner part of the wings, whilst the broad outward parts of the same have turned yellow or orange-red, the latter color appearing on the hind wings, where the orange-red coloring of the wing-cells which in various other species of the *Asterias* group has been specially developed on the under-surface, attains great importance also on the upper surface.

The black *P. Turnus Glaucus* ♀ is as compared with the common bright female type of *Turnus* a more southern form living in warmer regions, so that here also climatic conditions seem to be decisive of transformation. This does not hold, however, for the dark *Asterias*, for these occur also in colder regions. Since female preponderance is determinative of the transformation in *Turnus Glaucus* and in *Bairdii*, and since this transformation corresponds entirely to that of *Asterias*, therefore the influences upon the weaker female sex which in this case is more sensitive must be sought as the cause of the transformation, and the more so because *Glaucus* ♀ appears also in the North in isolated cases among the common *Turnus*.

The facts here presented also afford a conspicuous example of the ease with which mimicry may erroneously be assumed and notoriously has been assumed by writers who need it in its full extent for the substantiation of their hypotheses. In the many various species of the *Asterias* group we should have the most beautiful instances of mimicry imaginable, were it not that these species have developed and are now living entirely without biological connexion. What perfect specimens of mimicry *P. Turnus Glaucus* ♀, *Asterias*, *Bairdii*, etc., would present to the enthusiastic devotee if he could only furnish the facts of biological connexion! Finally, in strict agreement with the instances which the devotees of mimicry have put forward, not only all the members of the *Asterias* group but also all of the *Machaon* and all of the *Turnus* groups must be regarded as mimetic. And I should scarcely be surprised if Pseudo-Darwinism were really to advance this contention.

It will immediately be evident to the unprejudiced observer, however, that the resemblances are the result of developmental

tendencies, and that independent sameness of development or homöogenesis is determinative of likeness, even in not immediately related forms.

As a fact, there is no doubt in my mind, that when the data have been carefully sifted, it will certainly be shown that by far the greater majority of cases of so-called mimicry have nothing to do with adaptation. It was to this purport that the entomologist Hahnel spoke long ago, from actual numerous observations which he had made in South America in nature; whereas Erich Haase[1] without having looked to actual nature at all, has recently set up no end of cases of mimicry on the basis of outward similarity between butterflies, and wrote a whole book on the subject. But it stands to reason that resemblances of this character, quite apart from the question of their origin, can prove nothing for adaptation. The demonstration of adaptation in nature itself is alone decisive.

As to the origin of actual cases of mimicry the same cannot possibly be explained by selection, and what Herr Weismann has recently said[2] about *Kallima* as a marvellous product of selection loses all its demonstrative force when opposed to the plenitude of facts which go to show that orthogenesis everywhere determines the shaping of characters and is in this manner enabled to produce the resemblance to a leaf on the under-surface of a butterfly, and that homöogenesis is able to bring about the greatest resemblance between two butterflies which do not live together at all—a phenomenon of which numerous cases are known.[3] There is similarly nothing marvellous about the systematic and proportionate extension of the leaf-marking of *Kallima* from the fore wing to the

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[1] Erich Haase: *Untersuchungen über die Mimicry auf Grundlage eines natürlichen Systems der Papilioniden.* Kassel, 1894.

[2] International Congress of Zoologists at Leyden, Sept. 16, 1895. *The Monist*, Jan., 1896. *Germinal Selection*, Chicago, 1896.

[3] Piepers in the entomological section of the Leyden Congress of 1895 referred to cases of this kind. Thus, *Junonia Asterie* of Java is like our *Hipparchia Megæra*, and *Junonia Erigone*, of the same locality, resembles our *Hipparchia Egeria*, so that in both cases mimicry would would have been assumed if the like butterflies had lived together. Further facts will be given later.

hind wing while skipping the posterior margin of the fore wing so far as this is covered by the hind wing. The same phenomenon is everywhere noticed and is obviously a consequence of the action of light or of lack of light. Selection can create nothing new. It can only work with what is already present. Once the similarity of the wings of a butterfly to a leaf has been produced, it can be useful and further development can then doubtless be favored by selection. The origin of the resemblance, however, cannot be due to accidental variation, which is supposed to have all possible characters ready for selection. *Kallima's* resemblance to a leaf is determined by a thousand and one details. Not one accident but a thousand accidents *together* would have been requisite, and would have had to present themselves suddenly, in order to produce this resemblance by the selectional agency of Darwinism. The resemblance to a leaf could not have gradually arisen by selectional means; it must have originated suddenly and in approximate perfection in order to have given selection any hold for its operations.

There is no chance in the transmutation of forms. There is unconditioned conformity to law only. Definite evolution, orthogenesis, controls this transmutation. It can lead step by step from the simplest and most inconspicuous beginnings to ever more perfect creations, gradually or by leaps; and the cause of this definite evolution is organic growth.

TH. EIMER.

TUEBINGEN.